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Grinnelian and Eltonian niche conservatism of the European honeybee (*Apis mellifera*) in its exotic distribution

AM MEDINA, M ALMEIDA-NETO

Departamento de Ecologia, Laboratório de Interações Ecológicas e Biodiversidade, Universidade Federal de Goiás, Goiânia, Goiás, Brazil

Abstract

The understanding of how niche-related traits change during species invasion has prompted what is now known as the niche conservatism principle. Niche conservatism predicts that species are prone to not change during invasion of new areas and most studies that have tested the niche conservatism principle have focused on the extent to which the species' climatic niches remain stable in their exotic distribution. However, it is equally important to address how biotic specialization, i.e. resource use, changes during exotic species invasions. Here, we use the widespread European honeybee (*Apis mellifera*) to understand whether its Grinnelian and Eltonian niches changed in its exotic distribution using tests of abiotic and biotic niche conservatism. We found that both niche domains of the European honeybee remained stable in its exotic distribution, which means that neither the climatic niche nor the biotic specialization showed significant differences between the native andthe exotic ranges. Our findings that climatic and resource use are coupled can be explained by *A. mellifera*'s long history of domestication and the possibility that life history traits (e.g., polyandry) may have shaped this species' large niche over the course of evolution and therefore facilitated exotic ranges colonization.

Introduction

One of the main questions explored in invasion ecology is that of how exotic species become successful in their exotic ranges. The most used explanations to determine the success of invasion are competitive superiority, disturbance, biotic resistance, mutualistic facilitation and enemy release (Lowry et al., 2013). Another potential explanation is that successful exotic species have some sort of phenotypic plasticity (Davidson et al., 2011) that helps them to shift their niches during the colonization of new areas. On the other hand, some studies have shown support for the niche conservatism hypothesis (Wiens et al., 2010) in the context of species' invasions, which predicts that exotic species retain traits related to their niches during the colonization of new areas (Petitpierre et al., 2012; Aguirre-Gutiérrez et al., 2014; Guisan et al., 2014; Faleiro et al., 2015; but see: Atwater et al., 2018).

A species' niche can be divided into two broad components: the Grinnellian domain, which corresponds to how a species depends on certain environmental conditions and tolerates variations in such conditions; and the Eltonian domain, which corresponds to how a species interacts with other species and uses its biotic resources (Soberón & Nakamura, 2009; Soberón, 2007). Both domains play a role in how an exotic species colonizes new areas. For example, an exotic species needs to tolerate the climatic conditions ofits exotic range and interact with different sets of antagonistic and mutualistic species (Guisan et al., 2014; Richardson et al., 2000). However, there is a bias in the literature toward the Grinnelian domain, specifically in those studies that have evaluated the niche conservatism hypothesis (Aguirre-Gutiérrez et al., 2014; Parravicini et al., 2015), wherein much less attention was paid to the Eltonian domain (but see Olalla-Tárraga et al., 2017).

A more comprehensive understanding of niche conservatism can be achieved if both the Grinnellian and the Eltonian domains were evaluated at the same time (Larson et al., 2010) rather than assuming they are congruent (Soberón & Nakamura, 2009). Under niche conservatism, the importance of environmental conditions in limiting the spread of exotic species will depend on the extent to which environmental conditions are different between native and exotic ranges. The higher the difference in environmental conditions between native and exotic ranges, the higher the chance of a difference between the native and exotic ranges of a species' realized climatic niche; if this difference is high, then the species is under niche shift (Hill et al., 2017). Furthermore, if the same rationale of niche conservatism applies to the Eltonian domain, then the resource specialization of a species in its exotic range should not be higher than its resource specialization in its native range (Emer et al., 2016). On the other hand, an increase in the set of resources used indicates biotic niche expansion; actually, this is analogous to the interaction release hypothesis (Traveset et al., 2015), whereby a colonizing species acquires new interactions due to the absence of competitors or predators.

In the present study, we used the European honeybee *Apis mellifera* Linnaeus, 1758 (Hymenoptera, Apidae) to evaluate whether limits in the exotic distribution of a widespread species can be explained by the Grinnelian and Eltonian domains of niche conservatism. If the Grinnelian niche is conserved, then we could expect that the honeybee would not expand its climatic niche in exotic ranges in comparison to native ranges. Alternatively, if the Eltonian niche is conserved, then we could expect to find that the honeybee would be restricted in terms of the number of plants that it could visit in exotic ranges in comparison to native ranges. Therefore, on the biogeographic scale, it is expected that the honeybee would interact with fewer plant lineages in its exotic range than in its native range. Additionally, at the local scale, the honeybee would have a smaller niche breadth in its exotic distribution in comparison to its local niche breadth in its native distribution. *A. mellifera* is a particularly good model organism because of its widespread distribution, super generalist behavior (Norfolk et al., 2018), and importance to the pollination of plants in natural habitats (Hung et al., 2018).

Methods

Grinnelian niche

We gathered *A. mellifera*' soccurrences using the Global Biodiversity Information Facility database (GBIF.org 2017) and retrieved a total of 88.653 points. Afterward, we removed occurrences without geographic coordinates and duplicated points, ultimately keeping 19.416 points (Fig 1a). We separated these occurrence data for the analysis of climatic niche on a native set (Africa, Europe, and Middle East) and an exotic set (Americas, Asia, and Oceania) because *A. mellifera* is native to Africa, Europe, and the Middle East, but has exotic

populations in Americas, Asia and Oceania (Han et al., 2012; Moritz et al., 2005). We considered island populations in the Seychelles and Mauritius as native because there is genetic evidence of *A. mellifera* subspecies colonization before human settlements in these regions (Techer et al., 2017). We opted to neglect *A. mellifera* subspecies differences because subspecies are known to interbreed (Schneider et al., 2004), and no data was available to incorporate subspecies information in the climatic and biotic analyses.

We downloaded bioclim variables from WorldClim (Fick & Hijmans, 2017) with a spatial resolution of five minutes (ca. 10 km² at the Equator line) and selected variables with correlations less than 0.8 to avoid multicollinearity. We selected the following variables: annual mean temperature (bio 1), mean diurnal range (bio 2), temperature seasonality (bio 4), annual precipitation (bio 12) and precipitation seasonality (bio 15). Variations in temperature are predictors of visitation frequency by *A. mellifera* (Hung et al. 2018), and should, therefore, be good predictors of the climatic niche of the species.

We used the framework developed by Broennimann et al. (2012) to analyze climatic niche; this approach uses both the climatic space occupied (occurrences) and the climatic space available (background) to create an environmental principal component analysis (PCA-env). The first axis of the PCA-env accounted for 48.55% of the variation of the climatic variables while the second axis accounted for 32.16% of the variation. Contributions of each environmental variable to the axis of the PCA-env are shown in Figure S1. This PCA-env allows for the comparison of the climatic niches of a species in two regions, taking three components into consideration: niche stability, niche expansion, and niche unfilling (Guisan et al. 2014). Niche stability is the portion of the analogue climatic space available in both ranges used by a species. Niche expansion is the portion of climatic space that a species uses in a new region but does not use in the other. Lastly, niche unfilling is the portion of climatic space that is present in both regions but is not used by the species.

In order to evaluate the Grinnelian niche conservatism we used niche similarity and equivalency tests (Warren et al., 2008). Niche similarity randomizes the distribution of the exotic range, keeping the native range fixed and calculates the probability that niche overlap is caused by a random distribution in the exotic range. Niche equivalency randomizes the distribution in both the native and exotic ranges and calculates the probability that niche overlap is caused randomly. We performed the PCA-env, niche similarity test, and niche equivalency test using the R package *ecospat* (Broennimann et al., 2015; Di Cola et al., 2017).

Eltonian niche

We gathered 108 plant-pollinator networks that included *A. mellifera* from the Web of Life: ecological networks database (www.web-of-life.es). Also, we complemented these networks with a non-systematic search that yielded 16 plant-pollinator networks and plant-pollinators inventories. The combination
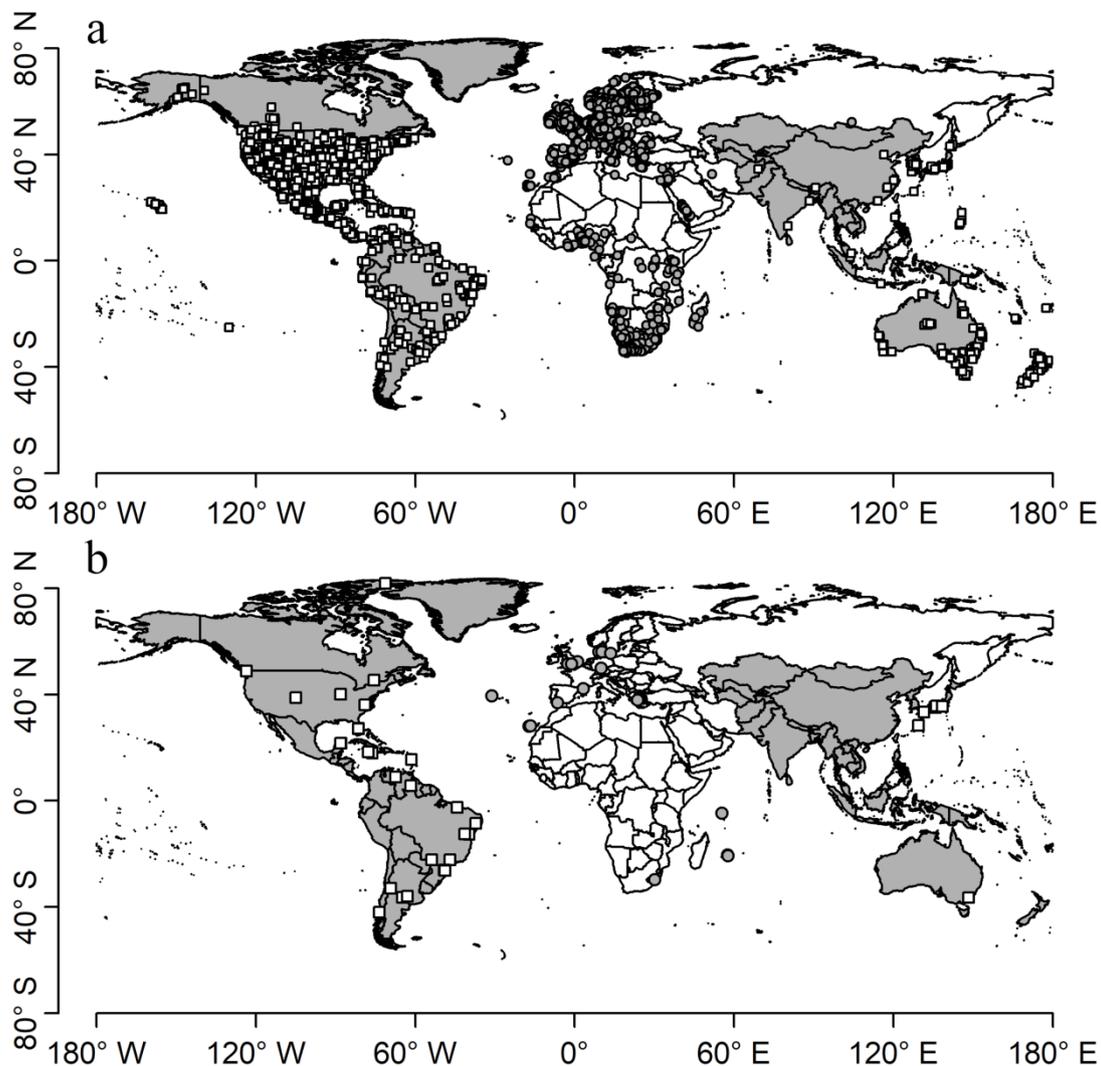
Fig 1. World map with the geographic distribution of the *Apis mellifera* Linnaeus, 1758 dataset. Areas in grey denote exotic distribution, and white areas denote native distribution. Exotic occurrences are indicated by white squares, and native occurrences are indicated by grey circles (a). White squares indicate networks in which *A. mellifera* is exotic, while grey circles indicate networks in which *A. mellifera* is native (b).

of both data sets resulted in a total of 124 plant-pollinator networks (Fig 1b; see Table S1 for references). Using these networks, we measured *A. mellifera*'s niche breadth using the standardized degree, a measure of dietary specialization which takes into account how many plants were visited by *A. mellifera* divided by the number of plants used by all pollinators (including *A. mellifera*). The standardized degree had the benefit of reducing the effects of networks with different sampling efforts because sampling effort can affect the richness of plants and pollinators found in networks.

To measure the phylogenetic diversity of plants consumed by *A. mellifera*, we used the Phylomatic tool (Webb & Donoghue, 2005) to build a phylogenetic tree for the 1843 plant species found in the plant-pollinator networks based on the megatree of the phylogenetic hypothesis of the Angiosperm Phylogeny Group (*R20120829*). Plants identified only at the genus (n=121) or family (n=32) levels were inserted as polytomies. We used the phylogenetic tree to calculate the mean phylogenetic distance of plants used by *A. mellifera* and the total mean phylogenetic

distance of the network using the *picante* R package (Kembel et al., 2010). For each plant-pollinator network, we calculated a standardized phylogenetic distance of plants used by *A. mellifera* by dividing the mean phylogenetic distance used by *A. mellifera* by the total mean plant phylogenetic distance. Mean phylogenetic distance was not measured in four exotic networks and 30 native networks because *A. mellifera* used only one plant in each of these networks.

At the biogeographic level, we compared the similarity between plant lineages used by *A. mellifera* in its native range and plant lineages used by *A. mellifera* in its exotic range by pooling all plants used in the local networks for both ranges. We measured the species phylogenetic similarity using the phylosor index in the *betapart* R package (Baselga et al., 2013). We partitioned the phylogenetic similarity into two components: the turnover component, corresponding to the Eltonian niche shift of the plant lineages visited by *A. mellifera*; and the richness component, corresponding to the Eltonian niche expansion or unfilling of these plant lineages.
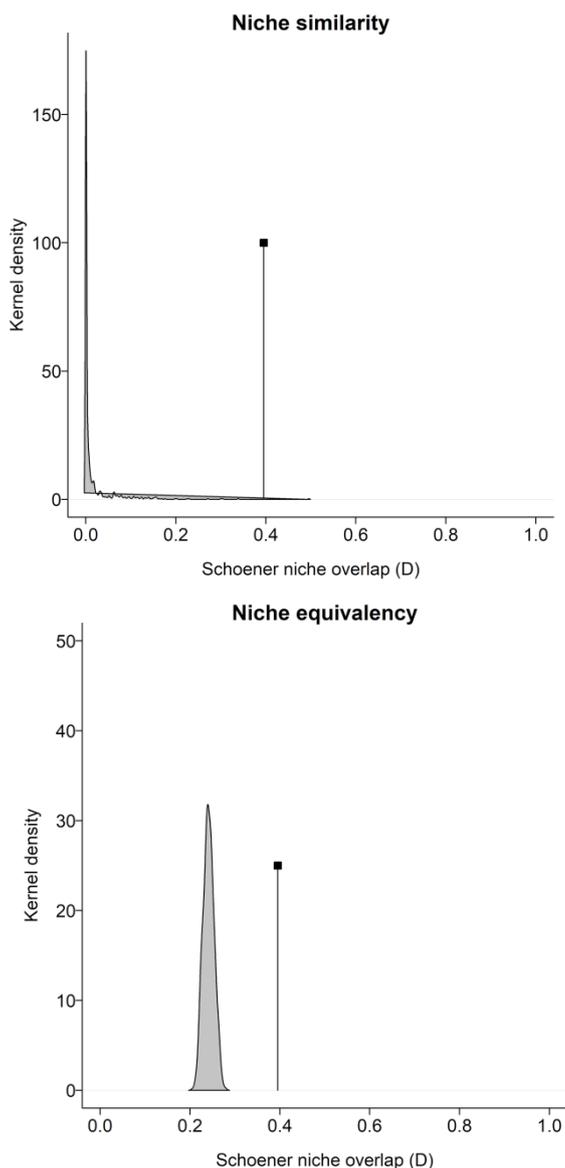
We tested the Eltonian niche conservatism of *A. mellifera* using two different scales. On the biogeographic scale, a permutation test was used to determine the similarity (three components) between plant speciesused by *A. mellifera* in its native distribution and plant species used by *A. mellifera* in its exotic distribution. This permutation was akin to the niche similarity test *sensu* Warren et al. (2008), which tests if the plant species used in the exotic range was different from that which occurred in a random invasion. Therefore, the use of plants by *A. mellifera* was randomized in the exotic rangeand kept fixed, in the native range. Furthermore, the richness of plant species used by *A. mellifera* in the exotic range was kept fixed and plant species were kept in their original distributions (native or exotic). On the local scale, the effect of *A. mellifera*'s range on the standardized degree and standardized mean phylogenetic distance was evaluated using two ANOVAs. All analyzes were performed in the R Programming Environment (R Core Team 2017).
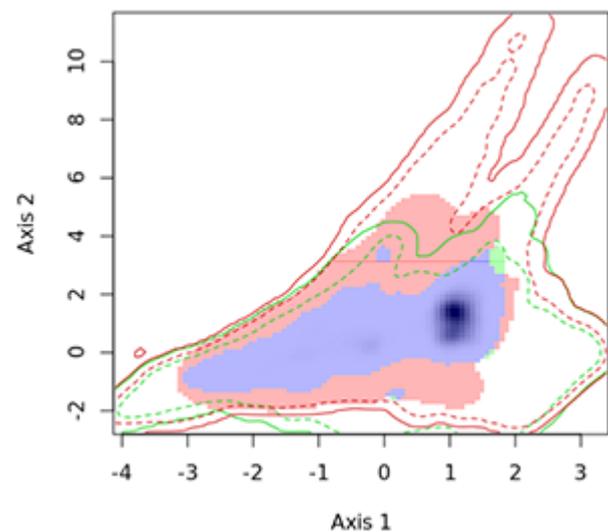
Results

Grinnelian niche

The climatic niche of *A. mellifera* in its native range was more similar to its climatic niche in its exotic range than expected through random invasion (Schoener overlap D = 0.395; $p < 0.01$; Fig 2). The same trend was found in the results of the niche equivalency test, in which both climatic niches were randomized ($p < 0.01$; Fig 2). The climatic niche was highly stable between both distributions (niche stability = 91.94%; Fig 3), with a low niche expansion in the exotic range (8.06%) and almost no niche unfilling (0.04%).

Fig 3. Climatic environment based on a principal component analysis of the environment (PCA-env) of *Apis mellifera* Linnaeus, 1758. The blue polygon corresponds to niche overlap, the red polygon corresponds to niche expansion, and the green polygon corresponds to niche unfilling. Solid lines represents the total native (red) and total exotic (green) ranges and dashed lines represents 75% of the ocurrences of native (red) and exotic ranges (green).

Eltonian niche

On the biogeographic scale, we found that *A.mellifera* used 50.39% of the available plants in its native range; whereas it only used 25.36% of the available plants in its exotic range. Furthermore, phylogenetic similarity was lower than that expected from a random invasion (Phylosor = 0.499; $p < 0.001$). Specifically, the turnover component of phylogenetic similarity was higher than expected from a random invasion (Phylosor = 0.341; $p < 0.001$), while the richness component of phylogenetic similarity was lower than expected from a random invasion (Phylosor=0.159; $p<0.001$).

On the local scale, we found that the standardized degree did not differ between native and exotic distributions ($F_{1, 167}$ = 0.0036; $p = 0.952$; Fig 4a). Furthermore, we found that the mean phylogenetic distance of plant resources used by *A. mellifera* did not differ between distributions ($F_{1, 133}$ = 0.369; $p = 0.545$; Fig 4b).

Fig 2. Niche similarity test and niche equivalency test comparing *Apis mellifera* Linnaeus, 1758 climatic niche overlap between its native and exotic ranges using 1000 randomizations of the exotic range. In the niche similarity, only the native range was randomized while in the niche equivalency test both ranges are randomized.
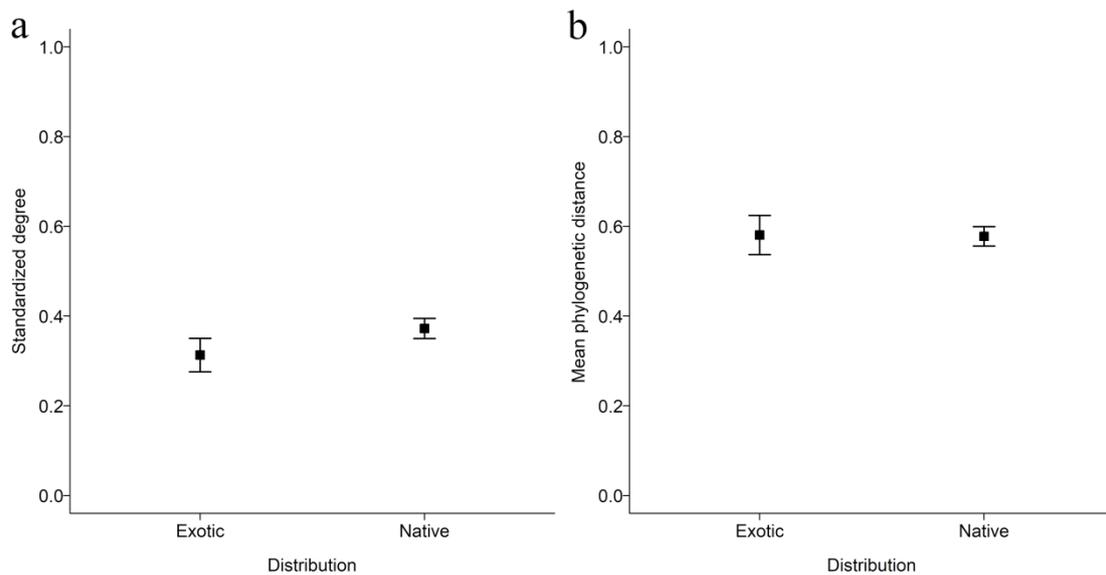
Fig 4. Effect of distribution on *Apis mellifera*'s Linnaeus, 1758 resource use in plant-pollinator networks. Standardized degree of plants used by *A. mellifera* (a). Mean Phylogenetic distance (MPD) of plants used by *A. mellifera* (b). Square indicate means and vertical bars indicate standard errors.

Discussion

The climatic niche of *A.mellifera* in its native range was conserved during its invasion of new ranges. This finding is in line with results of previous studies that showed evidence of niche conservatism in *A. mellifera* subspecies (Vital et al., 2012). This honeybee species has a long history of domestication by human populations (Bloch et al., 2010), which has helped the species achieve a global distribution and increased genetic diversity due to admixture (Harpur et al., 2012; Wallberg et al., 2014). In parallel, *A. mellifera* is among the most polyandrous of social insects, and this pattern increases population genetic diversity. An increase in genetic diversity buffers colonies from diseases (Tarpy, 2003) and may also help *A. mellifera* occupy different climatic conditions. Indeed, polyandrous colonies accumulate resources faster and have higher rates of winter survival than their monoandrous counterparts (Mattila & Seeley, 2007). Furthermore, introductions of multiple subspecies can boost the spread of honeybees and the success of colonization (Schneider et al., 2004), because phenotypic differences may help in the colonization of regions with different environmental conditions.

We also found that *A. mellifera* conserved its Eltonian niche on the regional and local scales. Because *A. mellifera* uses a broad range of plant species in its native and exotic distributions, *A. mellifera* can interact with a similar number of plants found in a particular climatic region after the climatic barriers are overridden (Emer et al., 2016). Indeed, one study has shown that plants with two different modes of pollination (hummingbirds and bats) had similar climatic niches because their pollinators' climatic niches did not differ (Alexandre et al., 2017). Therefore, if the climatic niche of *A. mellifera*

overlaps with that of most of other native pollinators, then the possibility of interactions with other native pollinators' host plants will increase. Changes in community species richness may lead to a niche shift in pollinators due to mutual competition (Fründ et al., 2013).

Additionally, if *A. mellifera* visits plant species with different floral traits from multiple lineages in its native range, then the possibility of interaction with native plants outside its native range will increase. Indeed, previous studies have shown that pollinator overlap was higher for exotic plants with traits more similar to those of native plants (Gibson et al., 2012; but see: Montero-Castaño & Vilà, 2017) and that *A. mellifera* can incorporate exotic plants in its diet (Montero-Castaño & Vilà, 2017). The ability of *A. mellifera* to use pollen from various plants to produce honey is demonstrated by the global increasing trend in honey yield (Aizen & Harder, 2009), notwithstanding crops pollination and fruit set are higher with pollination driven by wild insects than compared to honeybee visitations (Garibaldi et al., 2013). Moreover, even with the ongoing scenario of *A. mellifera* importance to agriculture is important to carefully understand possible impacts to native species, especially considering that honeybees can consume pollen much faster than native species (Cane & Tepedino, 2017). Besides competing for resources, invasive pollinators can transmit pathogens, cause reproductive disruptions of native bees and modification of native plants communities (Stout & Morales, 2009). For example, honeybee spillovers from cultivated areas to native woodlands can have negative effects in the structure of plant-pollinator networks and seed set of native plants (Magrach et al., 2017).

Our finding that the niche expansion of *A. mellifera* was below 10% differs from the results of a recent review (Hill et al., 2017) that showed that most invasive insects often undergo

niche shifts during the invasion process. Indeed, *A. mellifera* differs from other insects in that it is actively spread through human beekeeping activities but can also spread by accidental releases in the wild, as was the case in the American continent (Moritz et al., 2005). Furthermore, we found major support for niche conservatism congruence between the Grinnelian and Eltonian domains. However, this finding should not encourage disregard for the Eltonian domain. Previous studies have shown that interactions are not irrelevant as predicted by the Eltonian niche hypothesis (Araújo et al., 2014) and that domains can be decoupled (Larson et al., 2010). The next step for future research is to gain an understanding of how the anthropogenic domestication of *A. mellifera* has shaped the species' niche over the course of evolutionary time and whether this domestication played a role in the coupling of the Eltonian and Grinnelian domains.

Authors contribution

AM MEDINA conceived the idea; AM MEDINA collected the data; AM MEDINA and M ALMEIDA-NETO interpreted and analyzed the data; AM MEDINA and M ALMEIDA-NETO wrote the manuscript and both approve the final version of the manuscript.

Acknowledgments

Supplementary Material

http://periodicos.uefs.br/index.php/sociobiology/rt/suppFiles/4901/0

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